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ARTICLE



Exploring the relationship of phase and peak-frequency EEG alpha-band and beta-band activity to temporal judgments of stimulus duration

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ABSTRACT

Pre-stimulus phase has been shown to influence temporal judgments concerning order, causality and simultaneity. One hypothesis is that phase cycles frame discrete perceptual snapshots over time. Yet, existing studies have explored the effect of pre-stimulus phase on fine-grained temporal judgments whereas no study has shown whether pre-stimulus phase influences sub-second temporal judgments lasting several phase cycles. If effects of phase on fine-grained temporal judgments reflect perceptual framing, then the perception of longer intervals might show some dependency on the frequency of phase cycles. Higher frequencies should promote increased temporal resolution and discrimination. We tested the relationship between the phase and frequency of oscillations and temporal judgments for longer durations. Participants judged the relative duration of two successive intervals lasting several phase cycles each. Pre-stimulus alpha-band and beta-band phase was associated with subsequent temporal judgments, although not sensitivity, therein providing evidence that pre-stimulus phase is related to temporal judgments that span a longer time-scale than has been previously demonstrated. Although we report evidence that peak-frequency of the alpha-band is related to one measure of task performance, this study does not provide evidence that higher peak frequencies of alpha- or beta-band activity are related to improved duration discrimination of longer intervals.

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Neuronal oscillations; phase; frequency; temporal perception

Introduction

Changes in the phase of brain oscillations are hypothesized to reflect fluctuations in neuronal excitability (Buzsáki & Draguhn, 2004; Klimesch, Sauseng, & Gruber, 2009; Lindsley, 1952) with excitatory phases favouring improved sensory processing and subsequent perception. The probability of detection of near-threshold visual (Busch, Dubois, & VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009) and auditory (Rice & Hagstrom, 1989) stimuli depends upon the phase of pre-stimulus activity around the alpha band (7–14 Hz). Moreover, low-frequency oscillations (~2–10 Hz) align to temporally predictable input (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008) with the probability of detecting subsequent near-threshold stimuli being contingent on the phase of the entrained activity (Mathewson et al., 2012). These studies demonstrate the functional significance of periodic changes in the phase of oscillations.

A formative study (Varela, Toro, John, & Schwartz, 1981) demonstrated that the phase of alpha at the onset of two temporally-proximal visual stimuli

predicted whether they were perceived as occurring simultaneously or asynchronously. They argued this effect supported a ‘framing’ hypothesis in which alpha cycles reflect sequential discrete ‘frames’ of perception, despite our experience that perception is continuous. Thus when two discrete stimuli occur within the same perceptual frame they are more likely to be experienced as simultaneous rather than as temporally segregated. More recently, a number of findings consistent with this framing hypothesis have demonstrated effects of oscillatory pre-stimulus phase on fine-grained temporal judgments (Baumgarten, Schnitzler, & Lange, 2015; Chakravarthi & Vanrullen, 2012; Cravo, Santos, Reyes, Caetano, & Claessens, 2015; Milton & Pleydell-Pearce, 2016). These studies investigated temporal judgments at or shorter than the hypothesized frame duration, typically thought to involve the ~10 Hz (~100 ms) alpha cycle for visual stimuli (Cravo et al., 2015; Milton & Pleydell-Pearce, 2016; Varela et al., 1981). However, if phase effects on fine-grained temporal judgments are due to the fact that alpha phase cycles determine periodic moments

at which information from the environment is consciously updated, then the rate of this process should influence sensitivity to temporal discriminations occurring over longer time-frames. A faster frequency of conscious perceptual updating would allow more accurate perception of event timing by improving the temporal resolution of perception. This then provides a possible mechanism by which we might expect to see effects of oscillatory frequency on longer-lasting temporal judgments. Interestingly, two studies have reported an association between alpha frequency and performance on a two-flash discrimination task in which participants perceived two closely-timed flashes as either a single event or two discrete events (Coffin & Ganz, 1977; Samaha & Postle, 2015). For trials where participants correctly perceived two stimuli, pre-stimulus alpha frequency was higher. However, there is little evidence exploring the effect of alpha phase and frequency on longer-lasting temporal judgments of duration. To this end, intervals spanning several hundred milliseconds allow dual investigation of the effect of alpha phase and variation in the frequency of contiguous phase cycles on subsequent temporal judgments. Although paradigms employing longer durations may involve other mechanisms by which timing is estimated, if phase cycles do reflect the temporal resolution of perceptual experience then the frequency of such oscillations might be expected to carry some useful information for the task when intervals last several phase cycles but are still ~1 second or less. We therefore tested whether alpha phase and peak-frequency were related to temporal judgments of longer durations. Although our prediction of a frequency effect was based on the framing hypothesis, this study was not intended as a direct test of the framing hypothesis itself, rather we tested for a relationship between oscillatory activity and judgments of longer-lasting temporal durations. As the estimation of longer durations may involve multiple processes thought to be involved in interval timing (e.g. clock speed, memory or decision processes; for a review see Kononowicz, van Rijn, & Meck, *in press*), it is also possible that phase or frequency effects may be related to temporal judgments in ways that are distinct from a framing account. We were therefore interested in whether previously observed effects of phase on fine-grained temporal judgments might extend to longer

durations, and if so whether frequency effects may also be evident.

For duration discrimination of two successive intervals (~400 ms each), we investigated whether alpha phase at onset influenced the temporal judgment, and, if so, whether the peak frequency of alpha also influenced task sensitivity.

Materials and methods

Subjects and stimuli

16 participants (9 female) from 19–38 years of age ($M = 26.1$, $SD = 5.31$) took part in the experiment. All had normal or corrected-to-normal vision and gave written informed consent in accordance with the University of Bristol Faculty of Science Human Research Committee.

Judgments concerned the respective duration of two sequential intervals which were demarcated by the flashing of two green LEDs (peak wavelength: 565 nm; typical light output: 20 mcd) situated above and below a central fixation point. The LEDs were recessed within a 19.5 by 11 cm matt-black display box positioned at eye-level 70 cm from the observer (Figure 1). Both LEDs were 0.82° above and below fixation (whole stimulus array subtended 0.41° by 2.05°). The experiment was written using the psychophysics toolbox (Brainard, 1997).

Design

Participants judged the relative duration of the two visually-demarcated intervals of time. Each trial consisted of four 10 ms duration flashes, and all interval durations were specified from the onset of one flash to the onset of the next flash (Figure 1). The first flash marked trial onset followed by a pre-stimulus period (randomised 1400–1600 ms). The two target durations were demarcated by three sequential flashes. Duration 1 (D1) was the duration between the onset of the second and third flash, and Duration 2 (D2) was between the onset of the third and fourth flash (Figure 1). D1 was kept constant (400 ms), and only D2 was systematically altered. Participants decided whether a comparison interval (D2) was longer (N-key response) or shorter (B-key response; same hand was used for both responses) than the standard interval (D1). This paradigm avoids requiring participants to provide accurate verbal estimates or reproductions of

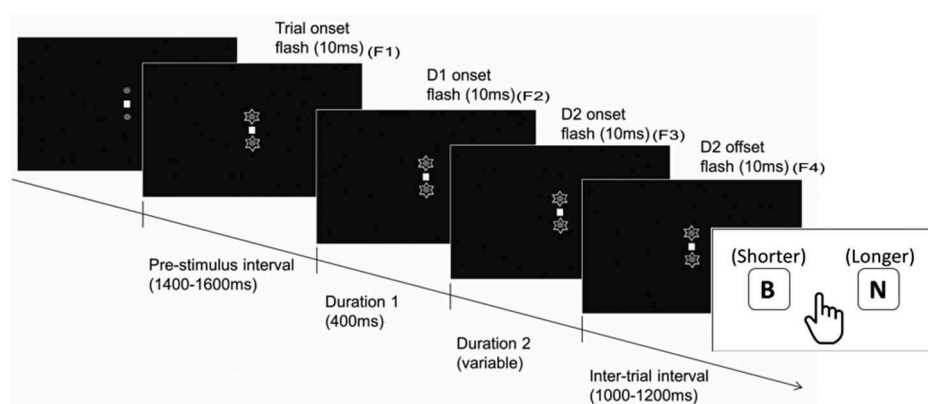


Figure 1. Sequence of stimulus flashes for one exemplary trial. Timings above the figure reflect the duration of each flash (from Flash 1: F1 to flash 4: F4), and timings below the figure indicate the durations denoted by the LED flashes. Participants indicated whether the comparison interval (Duration 2, D2) was shorter or longer than the standard interval (Duration 1, D1).

fine timescales, but as a judgment of successive stimuli it is associated with a time-order error (TOE) (Grondin, 2010). TOE is a bias where judgments about the strength of successive stimuli tend to display a specific and asymmetric bias for one stimulus. For this paradigm, the first interval is often perceived as longer than the second (Grondin, 2010) (discussed below).

The point of subjective equality (PSE) refers to the duration of D2 which elicits 50% of both Shorter and Longer responses. This duration is perceived as equal to D1 (400 ms); its similarity to D1 indicates participants' sensitivity to the task. As aforementioned, successive judgments introduce a TOE bias and the PSE is generally longer than D1 (known as 'time dilation' for perceived duration of D1) (Hellström, 1985; Kanai, Paffen, Hogendoorn, & Verstraten, 2006). This was therefore an expected outcome of the study and not the focus of interest. Despite the TOE, duration discriminations presented close to the PSE reflect near-threshold judgments, and we investigated whether response variation to such stimuli was influenced by the phase and peak-frequency of oscillations. Even with time dilation, oscillations may influence perceptual variation in the temporal judgment with certain phases associated with PSE values closer to the actual length of D1 (indicating better task sensitivity). However, a second estimate of sensitivity to the duration discrimination is given by calculating the slope of the response function to differences in the duration of D2. The effect of alpha phase and peak-frequency was therefore investigated for both the slope and the PSE.

The main experimental task employed a method of constants design with five lengths of D2 intended to

elicit 0.1, 0.3, 0.5, 0.7 and 0.9 proportion of Longer responses. As the durations associated with these conditions were expected to show individual variance, they were determined individually using a randomly interleaved double-staircase procedure before the main experiment. The two staircase stimuli started with a D2 duration of 200 ms and 600 ms respectively and initial step-changes in D2 length were 200 ms. For each staircase, the step-change in D2 was decreased every three response reversals through the following magnitudes: 200, 100, 50, 20, 10, 5 & 1 ms. After 100 trials (50 per staircase), a Weibull function was fitted to the results to derive their psychometric function. D2 conditions were the durations associated with 0.1, 0.3, 0.5 (PSE), 0.7 and 0.9 proportion of Longer responses. For the main analysis, we investigated trials from the 0.5 condition only so that the influence of phase and peak-frequency could be investigated on response variation to identical stimuli.

For the main experimental task, there were 100 trials for each of the 5 conditions of D2. Trials were presented in 5 blocks of 100 trials. Within blocks, 20 trials were presented from each condition, the order of which was randomised.

EEG acquisition and analysis

EEG data were recorded from 30 Ag/AgCl electrodes located in accordance with the International 10–20 system. These were referenced to two linked electrodes on the left and right mastoid. Vertical and Horizontal electro-oculogram recordings were taken from electrodes placed above and below the right eye (VEOG) and both outer canthi (HEOG). Electrode

impedances were kept <10 k Ω . Data was acquired using a Contact Precision amplifier with a highpass filter of 0.03 Hz and a lowpass at 200 Hz. Data was sampled at 1000 Hz and then downsampled and saved at 500 Hz. Subsequent data processing was undertaken in MatLab (The MathWorks, Natick). Offline, data were filtered using a first order Butterworth high pass filter with a cut-off at 0.1 Hz and a fourth order Butterworth low pass filter with a cut-off at 48 Hz. As analysis investigated pre-stimulus phase effects on subsequent perception, a causal filter was used in initial filtering to avoid backward contamination of post-stimulus evoked activity that could undermine any claims of causality (Zoefel & Heil, 2013). Although causal filters create phase delays that shift the signal in time (Widmann, Schröger, & Maess, 2015), the main concern of analysis was to assess whether there was an effect of pre-stimulus phase on subsequent perception as opposed to locating precise timing of any effect. Therefore no strong claims are made regarding the precise timing of effects. As ERPs influence phase measures (Zoefel & Heil, 2013), phase analysis focused only on a baseline period.

Broad trial epochs were initially defined as the period from 600 ms before onset of D1 to 100 ms post offset of D2. As blinks represent periods of visual insensitivity where stimulus flashes (10 ms) might be missed, we used artefact rejection. To identify trials contaminated by blinks or ocular artefacts, we used a template-matching procedure (Milton & Pleydell-Pearce, 2016). Epochs where activity exceeded ± 75 μ V were also removed from analysis on a per-electrode basis (e.g. Busch et al., 2009), and remaining trials were further subject to visual inspection for channels VEOG and HEOG to ensure no ocular activity was evident. Only the central condition was analysed in the primary phase analyses (D2 condition associated with a 0.5 proportion of Longer responses). The average number of trials per participant per electrode ($n = 30$) for analysed conditions (max 100) was 87.681 ($SD = 9.262$).

In line with previous findings (Cravo et al., 2015; Mathewson et al., 2009; Milton & Pleydell-Pearce, 2016; Varela et al., 1981), we predicted an effect in the alpha range (7–14 Hz, see Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014 for justification of this definition of the alpha-band frequency range), so analysis focused on a cluster of occipital electrodes

(O1, O2, POZ, OZ). An occipital cluster was chosen due to its relevance to the visual nature of the task, and because occipital electrodes have been previously demonstrated to be associated with phase effects on temporal judgments (Milton & Pleydell-Pearce, 2016; Varela et al., 1981), and previous effects of peak alpha-band frequency on two-flash discrimination have been reported at occipital electrodes (Coffin & Ganz, 1977; Samaha & Postle, 2015).

We first investigated pre-stimulus alpha amplitude to ensure alpha activity was present in the data. Alpha amplitude was computed using the fast Fourier transform (FFT) within a 600 ms pre-stimulus window prior to onset of D1 (–600 ms to –2 ms). This epoch was linearly detrended, had the DC component removed, was tapered and then zero-padded equally at either end so that it extended to 500 points (1000 ms). This gave a frequency resolution of 1 Hz. Amplitude was normalized relative to the mean amplitude of all frequency bins between 5–25 Hz.

The influence of pre-stimulus phase on temporal judgments was investigated in the same 600 ms epoch described above. This epoch ranged from –600 ms to –2 ms from stimulus onset and therefore does not contain any post-stimulus activity. This window was tapered (tukey cosine tapers on first and last 100 ms of the raw data) and then zero-padded equally at either end to allow an estimation of phase throughout the 600 ms without including post-stimulus activity. Instantaneous phase was computed in 1 Hz frequency steps from 5–48 Hz using Gabor filters of 3 cycles (for a similar approach see Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013). Phase on every trial was calculated for each frequency and time point at each electrode in the occipital cluster defined above. For each cluster electrode, trials were separated by perceptual response (Longer versus Shorter) and the mean phase angle for each was calculated. Equal trial numbers for the two perceptual responses were ensured by taking a random selection of trials from the larger response condition (this difference was small: mean absolute difference in trial numbers across perceptual response was 1.84 trials, $SD = 1.62$). For each participant, the cluster-level (second-order) mean phase angle for each perceptual response was calculated (Zar, 1999). Across-participant differences in the cluster-level mean phase angles for each response were then tested for each frequency and time point using

the non-parametric paired test for angular difference described by Zar (Zar, 1999) (see also Cravo et al., 2015) and controlled using non-parametric cluster-based permutation analysis (1000 permutations; entry-threshold $<.05$; cluster statistic threshold of $<.05$) (Maris & Oostenveld, 2007). Clusters in the original data could form on the basis of significant phase differences ($\alpha < .05$) being adjacent in frequency and/or time. The sum of all phase difference (R') values in the cluster was then computed. The significance of any cluster in the original dataset is then assessed by comparison to a Monte Carlo estimate of the permutation distribution. This involves the random partition of the data (the mean phase values associated with each perceptual response) into two new subsets that are then tested at each time-frequency point and any new clusters values are summed. This procedure is repeated 1000 times and the proportion of randomly partitioned datasets in which the cluster sum is larger than in the original dataset gives you the critical p value (for more detail see Maris & Oostenveld, 2007). As a double-check of this analysis, phase differences between perceptual responses were also evaluated using an alternative method (see Samaha, Bauer, Cimaroli, & Postle, 2015). Here, phase differences were assessed using the Watson-Williams test - using circstat toolbox (Berens, 2009), and corrected for multiple comparisons using fdr correction (matlab's mafdr.m). For post-hoc phase analyses, trials were separated into 5 phase bins (width $\pi/2.5$) starting with the first bin centred at 0 (trial numbers per bin: $M = 17.625$, $SD = 2.791$). The proportion of Longer responses for each phase bin was standardized by dividing by the average from all phase bins. The results were then analysed using a one-way repeated measures ANOVA with 5 levels of phase to look at the effect of phase bin on temporal judgment. This analysis was done at the time-frequency point of greatest significance and therefore reflects an upper-bound of phase effects, but allows comparison with the existing literature (Baumgarten et al., 2015; Busch et al., 2009).

Frequency information was calculated for three windows per trial (D1+D2: total duration of stimulus presentation; D1 only & D2 only). Three types of analysis were performed concerning these frequency measures. First, for D1+D2, condition-average ERPs were subtracted from each individual trial per

condition. As D2 duration varied with condition and participant, all epochs were zero-padded equally at either side so that the window extended to 700 points (1400 ms). This length captured all durations and ensured frequency bins were comparable across conditions and participants (resolution: 0.714 Hz). Per trial, FFT-derived amplitudes for frequency bins were stored. Trials were split by response and a difference in individual peak alpha frequency (IAF) was assessed for D1+D2 using a t test. IAF was calculated between frequency bins 7.143–14.286 Hz on the averaged spectrum of all trials for that response. To ensure reliable detection of peaks, IAF was defined using matlab's 'findpeaks' function where a peak needs to be larger than both its neighbouring points. This was calculated using the cluster-average spectrum.

As phase results revealed an effect of alpha-band and beta-band phase on perceptual outcome (see *Results*), analysis of individual beta frequency (IBF) was also undertaken. IBF was calculated using the procedure outlined in Haegens et al. (2014). Using least-squares linear regression, the $1/f$ component of the log-transformed spectrum (15–25 Hz) was modelled and subtracted from the spectrum to allow more reliable detection of the peak (again using findpeaks.m) frequency in the beta range (15–25 Hz).

The second test of frequency determined IAF and IBF as above but trials were not separated by response. We assessed the correlation between individuals' IAF and IBF during stimulus presentation (D1 +D2) and their PSE and the slope of their psychometric function. This allowed us to assess whether peak-frequency differences across participants were associated with sensitivity to duration discrimination.

Third, the effect of any difference in peak-frequency between D1 and D2 was assessed on the proportion of Longer responses. For this analysis, trials were split by response and the peak frequency was detected on the average spectrum across all trials (per participant and electrode) for D1 only and D2 only. The difference was described as IAF in D1 only minus IAF in D2 only. This was also computed for IBF. Using paired t -tests, we evaluated whether responses were associated with differences in the frequency difference between duration D1 and D2.

Finally, further tests of amplitude effects on the temporal judgment were made using the FFT output from the pre-stimulus epoch outline above (–600 ms to –2 ms), and the FFT output from D1 and D2 that

was generated in determining peak-frequency effects. Alpha- (7–14 Hz) and beta-band (15–25 Hz) frequency bins were averaged for each time region (pre-stimulus, D1 & D2) and a two-factor repeated measures ANOVA was used to assess whether amplitude varied according to temporal judgment (Longer vs. Shorter) and time region.

Standard errors include repeated measures correction (Morey, 2008) and Greenhouse-Geisser correction was used for ANOVAs where sphericity was violated.

Results

Behavioural data

Preliminary task

The staircase task was used to derive the 5 conditions of D2 duration used in the main task. These were associated with 0.1, 0.3, 0.5, 0.7 and 0.9 proportion of Longer responses. The average duration for the 0.5 condition (PSE) was 483 ms ($SD = 98$ ms) (Figure 2(a)). This indicates an average time dilation, but 2 participants showed time compression (PSE: $M = 383$ ms, $SD = 2$ ms).

Experimental trials

The average proportion of Longer responses to the five D2 conditions were 0.091, 0.215, 0.481, 0.707 and 0.819 ($SE = 0.032, 0.041, 0.023, 0.034$ & 0.036 , respectively). For investigating the effects of alpha activity

on temporal judgments, EEG analysis was restricted to the 'central' condition. The third D2 condition was designed to elicit 0.5 proportion of Longer responses and the average was close (0.481), but individual results were checked. The 'central' condition was denoted as the condition closest to 0.5 proportion of Longer responses. For 5 of the 16 participants, this was not the third condition, but one of its neighbours (lower neighbour for 1 and higher neighbour for 4 participants).

A one-way repeated measures ANOVA showed that the 3 levels of central D2 condition (Central -1, Central and Central+1) were associated with differences in the proportion of Longer responses ($F(1.217, 18.255) = 69.254$, $MSE = 0.026$, $p < 0.0001$, $\eta_p^2 = 0.822$; Figure 2(b)), and this confirmed that the D2 conditions did influence response outcomes as expected. The three central conditions (C - 1, C and C + 1 respectively) had average durations of 417 ms ($SE = 23$), 497 ms ($SE = 4$) and 589 ms ($SE = 23$).

Electrophysiological data

Pre-stimulus amplitude

Amplitude was checked in the pre-stimulus period to make sure there was appreciable alpha in the data and this is shown in Figure 3(a).

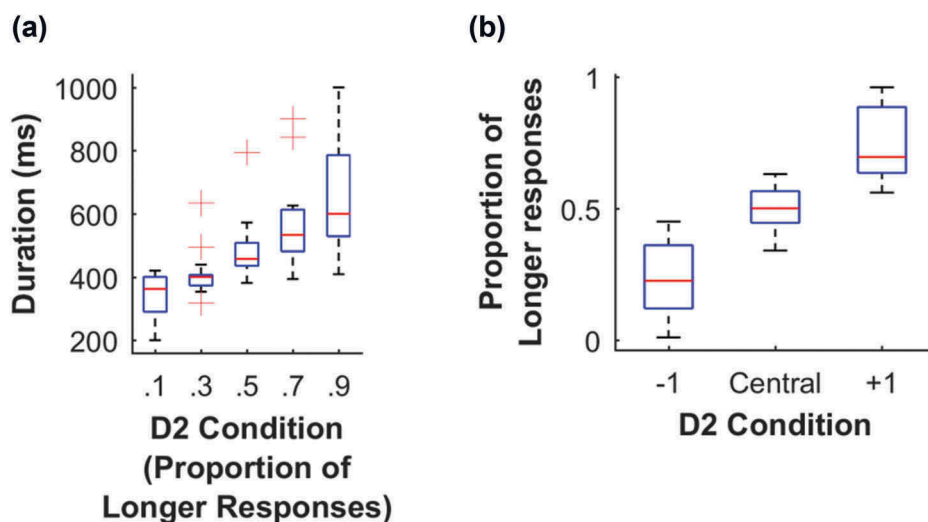


Figure 2. Behavioural results. (a) Duration (ms) of each D2 condition derived from the staircase task and used in the main experiment. (b) The proportion of Longer responses associated with the three 'central' conditions. The central condition refers to the respective condition of D2 duration associated with an individual proportion of Longer responses closest to 0.5. Whisker length for both plots is 1.5 times the interquartile range.

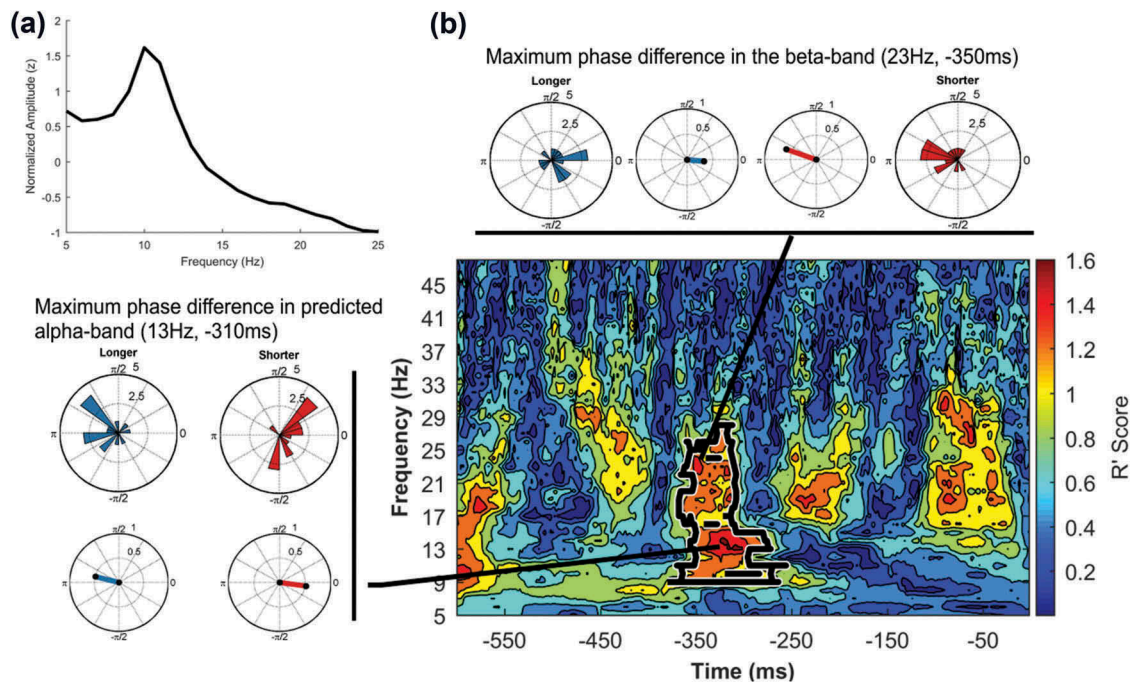


Figure 3. (a) FFT of the pre-stimulus normalized amplitude spectrum in the 600 ms period leading up to stimulus onset (time 0). It depicts the average of all electrodes in the occipital cluster (O1/2, POZ & OZ) and indicates a clear peak in the alpha band (7–14 Hz). Mean peak value: 10 Hz. (b) Time-frequency plot of phase differences between response outcomes in the 600 ms pre-stimulus period leading up to stimulus onset (time 0). Significant range is outlined in black (–380 ms to –256 ms, 9–28 Hz). The angle histograms extending from the main time-frequency plot show across-participant phase distributions and resultant vectors for the two temporal judgments (Longer responses in blue; Shorter responses in red). This is depicted for the maximum point of phase difference which was in the alpha-band (13 Hz) which was predicted, and for the maximum point of phase difference in the beta-band which was not predicted.

Pre-stimulus phase

Pre-stimulus phase was analysed at the occipital electrode cluster described in the Methods. In the pre-stimulus window (–600 ms to –2 ms), phase differences between Longer and Shorter temporal judgments were explored for frequencies 5–48 Hz using the non-parametric test of angular differences in paired data (Zar, 1999; see also Cravo et al., 2015), corrected with non-parametric cluster-based permutation analysis. This revealed phase differences between the two subsequent temporal judgments (Monte Carlo $p = 0.018$). Within this region and time, the difference in pre-stimulus phase was observed for frequencies in the alpha and beta range (9–28 Hz) between ~–380 ms and ~–256 ms with the strongest observed difference at 13 Hz (Figure 3(b)). Figure 3(b) also shows angle histograms for the two points of maximum phase difference within the alpha- and beta-band. This confirms our prediction of an association between alpha-band phase and the temporal judgment, although the association of beta-band phase was not predicted. An alternative analysis (Watson-Williams test corrected with

fd_r; see Methods) to double-check the results revealed phase differences in a similar time-frequency range with the same point of maximum phase difference (13 Hz, –310 ms).

For comparison with previous findings (Baumgarten et al., 2015; Busch et al., 2009), a post-hoc test explored the influence of phase on temporal judgments by separating trials into 5 phase bins at the time and frequency point where the effect was strongest for the alpha (13 Hz, –310 ms) and beta-band (23 Hz, –350 ms) (Figure 3(b)). As a post-hoc test at the strongest frequency and time points, this indicated an upper-bound of phase effects. We analysed both frequencies as the predicted outcome was in the alpha-band, but the results also encompassed phase differences in the beta-band. The influence of phase bin on the standardized proportion of Longer responses was assessed using a one-way repeated measures ANOVA. Results demonstrated a significant difference in temporal judgment for pre-stimulus alpha-band phase ($F(4,60) = 4.418$, $MSE = 0.029$, $p = 0.003$, $\eta_p^2 = 0.228$), and pre-stimulus beta-band phase ($F(4,60) = 2.873$, $MSE = 0.033$, $p = 0.030$,

$\eta_p^2 = 0.161$; Figure 4(a)). For 13 Hz (alpha-band), comparing the average standardized response of the two bins associated with the highest proportion of Longer responses versus the average standardized response of

the two phase bins associated with the lowest proportion of Longer responses revealed a difference of 16% (1.094 vs. 0.924). This is comparable with previous effects of pre-stimulus phase on visual detection (16%; Busch

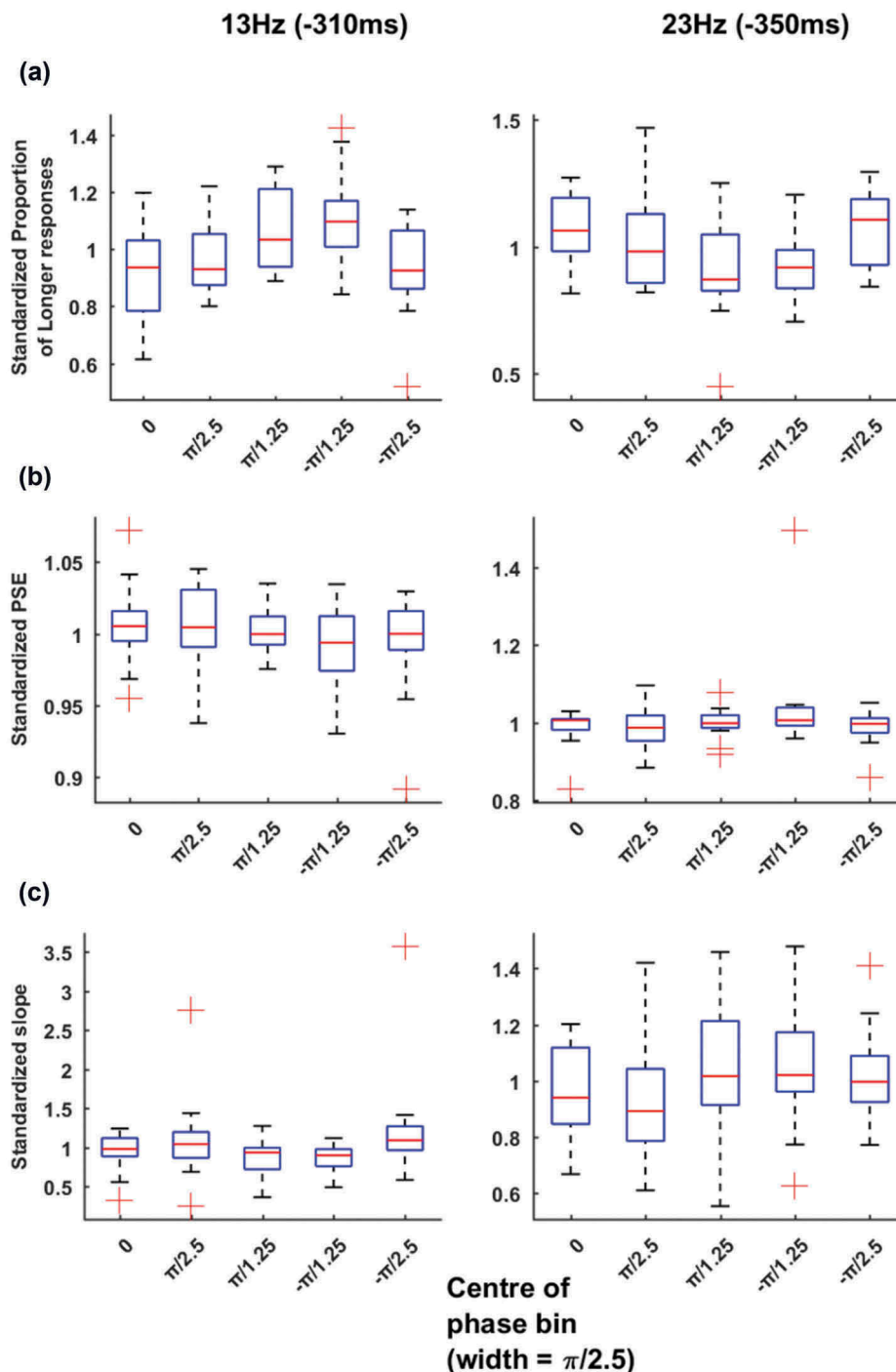


Figure 4. The relationship between pre-stimulus phase and the response and sensitivity to the temporal judgment. **(a) Left:** Standardized proportion of responses of Longer as a function of pre-stimulus alpha-band (13 Hz) phase bins. **Right:** Standardized proportion of responses of Longer as a function of pre-stimulus beta-band (23 Hz) phase bins. **(b) Left:** Standardized PSE as a function of pre-stimulus alpha-band phase bins. **Right:** Standardized PSE as a function of pre-stimulus beta-band phase bins. **(c) Left:** Standardized slope of participants' psychometric function as a function of pre-stimulus alpha-band (13 Hz) phase bins. **Right:** Standardized slope as a function of pre-stimulus beta-band (23 Hz) phase bins. For all plots, whisker length is 1.5 times the interquartile range.

et al., 2009) and tactile simultaneity (13%; Baumgarten et al., 2015).

Using the same phase bins, results showed no significant effect of pre-stimulus alpha-band phase ($F(4,60) = 0.765$, $MSE = 0.001$, $p = 0.552$, $\eta_p^2 = 0.049$) and no significant effect of beta-band phase ($F(1.426,21.388) = 1.235$, $MSE = 0.017$, $p = 0.297$, $\eta_p^2 = 0.076$) on standardized PSE (Figure 4(b)). Similarly, there was no effect of phase bins on the standardized psychometric slope for the alpha- ($F(1.817,27.250) = 1.900$, $MSE = .470$, $p = 0.172$, $\eta_p^2 = 0.112$) or beta-band ($F(4,60) = 1.043$, $MSE = 0.048$, $p = 0.393$, $\eta_p^2 = 0.065$; Figure 4(c)).

To check that phases from all trials (across both responses) were uniformly distributed, and that an overall non-uniform distribution was not biasing results, a Rayleigh test was performed at the strongest time-frequency point (13 Hz, -310 ms) for each participant and cluster electrode. No p value survived Bonferroni correction; uncorrected, 1 participant showed non-uniformity at one or the 4 electrodes in the occipital cluster. We assessed the probability of this finding when drawing trials from a random distribution of phases (Busch et al., 2009). Per subject and electrode, random phases equalling the number of trials in the data were drawn and assessed by a Rayleigh test. This was repeated 10,000 times to form a test distribution. The probability of at least 1 participant with ≥ 1 electrode deviating from uniformity (uncorrected Rayleigh test) was 0.964. Accordingly, the data is not thought to be systematically biased from uniformity.

Peak-frequency effects

Frequency effects for both the alpha- and beta-band were investigated given that alpha-band effects were the a priori interest but phase effects were also observed in the beta-band. First, we separated trials by response and investigated whether there was a difference in peak-frequency during stimulus presentation. For the alpha (7.143–14.286 Hz), responses were not associated with a statistically significant difference in frequency ($t(15) = -1.789$, $p = 0.094$, Hedge's $g_{av} = 0.370$) (Longer responses: $M = 10$ Hz, $SD = 1.278$; Shorter responses: $M = 10.491$ Hz, $SD = 1.243$). For the beta (15–25 Hz), responses were not associated with a statistically significant difference in frequency ($t(15) = -0.136$, $p = 0.893$, Hedge's $g_{av} = 0.036$) (Longer responses: $M = 20.580$ Hz, $SD = 2.365$; Shorter responses: $M = 20.670$ Hz, $SD = 2.411$).

Second, we looked at the across-participant correlation between frequency during stimulus presentation and PSE and slope. Based on the idea that phase cycles reflect periodic conscious updating, a faster rate should improve task sensitivity because it increases the perceptual resolution of time. As participant PSEs generally exhibited time dilation (see *Behavioural Data*) and were >400 ms (D1 duration), improved sensitivity for perceived duration is associated with a lower PSE. We therefore predicted a negative correlation. The data from one participant was excluded from this analysis because their PSE was greater than 2SD of the mean. The standard deviation for IAF (minus the outlier) was 1.278, and for IBF was 2.299. There was a positive association between within-stimulus IAF and PSE ($r = 0.572$, $p = 0.026$), but the association between IBF and PSE ($r = 0.251$, $p = 0.367$) was not statistically significant (Figure 5). It is worth noting that the IAF-PSE correla-

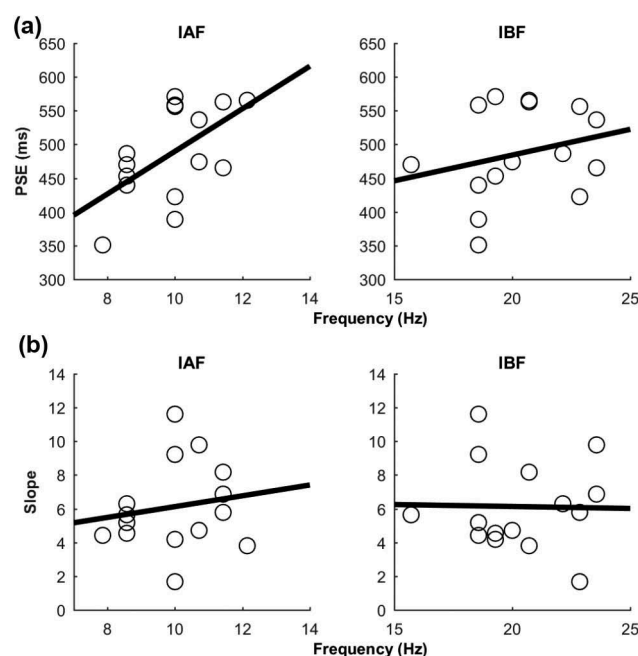


Figure 5. The relationship between frequency during stimulus presentation and sensitivity to the temporal discrimination. (a) Each participant's point of subjective equality (PSE) is shown in relation to their (left) individual peak alpha-band frequency (IAF; determined in the range 7.143–14.286 Hz) & (right) individual peak beta-band frequency (IBF; determined in the range 15–25 Hz). The least-squares regression line is plotted. (b) The value of the slope of participants' psychometric function is shown in relation to their (left) individual peak alpha-band frequency (IAF; determined in the range 7.143–14.286 Hz) & (right) individual peak beta-band frequency (IBF; determined in the range 15–25 Hz). The least-squares regression line is plotted.

tion was not in the predicted direction which we return to in the Discussion.

The association between peak-frequency and the slope of participants' psychometric function was not statistically significant for within-stimulus peak alpha- ($r = 0.162$, $p = 0.568$) or peak beta-band frequency ($r = -0.020$, $p = 0.943$).

Finally, we investigated whether responses were associated with any difference between the frequency during D1 and D2. For instance, were trials where frequency was higher during D2 than D1 more likely to lead to a response of Longer because more perceptual samples occurred within it?

Results showed no evidence that responses were associated with differences in the frequency difference between D1 and D2 for alpha ($t(15) = 0.100$, $p = 0.921$, Hedge's $g_{av} = 0.030$; Longer responses: M difference (D1-D2) = 0.045 Hz, $SD = 1.236$; Shorter responses: $M = 0$ Hz, $SD = 1.608$) or beta ($t(15) = -0.427$, $p = 0.676$, Hedge's $g_{av} = 0.155$; Longer responses: M difference (D1-D2) = 0.089 Hz, $SD = 3.288$; Shorter responses: $M = 0.667$ Hz, $SD = 3.811$).

Post-hoc amplitude analysis

As previous research on the perception of time has implicated beta power in the estimation (Kulashekhar, Pekkola, Palva, & Palva, 2016) and production (Kononowicz & van Rijn, 2015) of time, we analysed whether there were effects of alpha- and beta-band amplitude alongside those observed for phase.

A 2 by 3 repeated measures ANOVA investigating the effect of Response (Longer vs. Shorter) and Time region (pre-stimulus, D1 & D2) on amplitude was run for the alpha-band (7–14 Hz) and beta-band (15–25 Hz). For the alpha-band amplitude, there was no effect of Response ($F(1,15) = 0.026$, $MSE = 0.003$, $p = 0.874$, $\eta_p^2 = 0.002$), Time region ($F(1.319,19.784) = 2.525$, $MSE = 0.009$, $p = 0.121$, $\eta_p^2 = 0.144$) and no interaction ($F(2,30) = 1.010$, $MSE = 0.001$, $p = 0.376$, $\eta_p^2 = 0.063$). Similarly, no effect of Response ($F(1,15) = 1.127$, $MSE = 0.001$, $p = 0.305$, $\eta_p^2 = 0.070$), Time region ($F(1.423,21.349) = 2.737$, $MSE = 0.002$, $p = 0.102$, $\eta_p^2 = 0.154$) or interaction ($F(2,30) = 0.563$, $MSE = 0.0003$, $p = 0.575$, $\eta_p^2 = 0.036$) was observed for beta-band amplitude.

Discussion

This study investigated the influence of pre-stimulus phase on temporal judgments of relative duration and the results demonstrated that the phase of pre-stimulus alpha- and beta-band activity is associated with temporal judgments of stimuli that persist well beyond the time-frame of one alpha or beta cycle itself. We therefore provide novel evidence that pre-stimulus changes in oscillatory phase can influence temporal judgments. As the paradigm utilised durations of several hundred milliseconds, we also investigated whether pre-stimulus phase effects were accompanied by an influence of within-stimulus peak-frequency. We reasoned that if pre-stimulus phase effects were the result of temporal framing, then higher within-trial peak-frequencies might be associated with increased temporal resolution and improved task sensitivity. In the circumstances of this study, however, we did not observe the predicted association between peak-frequency and task performance, and we did not show a relationship between peak-frequency and temporal judgments or sensitivity to the task.

The results are consistent with a large amount of evidence demonstrating the functional significance of pre-stimulus phase changes in neuronal oscillations (Busch et al., 2009; Cravo et al., 2015; Mathewson et al., 2009; VanRullen, 2016). On the basis of findings from previous temporal paradigms (Cravo et al., 2015; Milton & Pleydell-Pearce, 2016; Varela et al., 1981) we expected an effect of alpha phase on visually-presented temporal judgments. Phase differences in alpha were evident, but effects were also observed within the beta-band which is consistent with evidence from other experimental paradigms, both visual and non-visual, that demonstrate phase effects outside the alpha range (e.g. ~15 Hz: VanRullen, Reddy, & Koch, 2005; beta: Baumgarten et al., 2015; 7 Hz: Busch et al., 2009; Hanslmayr et al., 2013). The results therefore align with the more general influence of oscillatory phase on perceptual outcomes that has been shown in the recent literature. Interestingly, the particular involvement of beta oscillations is consistent with the association of beta amplitude to temporal judgments in other timing paradigms (e.g. Kononowicz & van Rijn, 2015; Kulashekhar et al., 2016). The exact role of beta oscillations in timing tasks is not yet clear although it has been suggested they might underlie the accumulation of duration evidence

(Kulashekhar et al., 2016) or that they relate to starting parameters for decision processes (Kononowicz & van Rijn, 2015). Although our results did not show an effect of beta- or alpha-band amplitude, the results still implicate pre-stimulus oscillatory activity in timing tasks and give support to the proposed notion that early brain states play a role in the trajectory of temporal decisions.

Having observed an effect of pre-stimulus phase on temporal judgments, we also investigated the relationship between peak-frequency and temporal judgments in line with the idea that phase cycles might temporally frame perception and therefore a higher rate should increase sensitivity for discriminating the relative duration of two intervals. We observed that, across participants, the peak-frequency of alpha during stimulus duration was positively correlated with participants' PSE, but we found no evidence that it was related to the slope of their psychometric function (i.e. a measure of sensitivity to the relative duration discrimination) or their subsequent temporal judgment.

In this study, participants' PSE was generally longer than the objective 400 ms duration of D1. This 'time dilation' indicates a bias for perceiving the duration of D1 as longer than it actually was. This is consistent with the well-documented TOE bias (Hellström, 1985) where one of two equal durations that are presented successively is systematically perceived as lasting longer. The positive correlation between individuals' PSE and their alpha-band peak-frequency suggests that higher peak-frequencies are related to exaggerations of the time dilation effect and individual variation in the magnitude of perceived duration. Yet, we observed no evidence that peak-frequency alpha was associated with within-participant temporal judgments to the relative discrimination of durations presented near an individual's PSE threshold. It is interesting to consider these findings in terms of the "internal clock" model of interval timing (Treisman, 1963) and subsequent variants (for a review see Kononowicz et al., *in press*), where timing is suggested to comprise a multi-stage process involving all or some combination of the following components: a pace-maker/clock (providing "ticks"), an initiation switch, an accumulator of clock ticks, a reference/memory stage and a comparator/decision stage. The positive association between peak-frequency of the alpha-band and participants' PSE could equate alpha-band oscillations to the clock-speed of an internal pacemaker. More 'ticks' of the clock during D1 would lead to an exaggerated estimate or experience of its duration. However,

two points are problematic for this interpretation. First, the judgement was a relative discrimination of two durations. An increase in clock speed during both should therefore be associated with a higher resolution of perception and therefore a better ability to discriminate duration differences, but we observed no evidence for this. Second, we failed to observe an effect of frequency differences between D1 and D2 for responses of Longer and Shorter. If peak-frequency related to clock speed, we would have expected responses of Longer to have greater frequency in D2 relative to D1 and the reverse for responses of Shorter. As such, the results suggest that individual peak-frequency of alpha-band activity is related to the threshold around which responses fluctuate but not the fluctuation of responses themselves. The findings from this study therefore do not support our prediction that increased peak-frequency would be associated with improved temporal resolution and sensitivity to the duration discrimination. We would note cautious interpretation of our findings here, however, insofar as we demonstrate an absence of evidence rather than evidence against this prediction, and we would encourage future research to elucidate the nature of frequency effects for perceived duration and duration discrimination. The idea that individual differences in peak-frequency alpha are related to differences in the perceived magnitude of durations is certainly an intriguing preliminary finding and one that bears future investigation.

We also note that our frequency results are in contrast to previous results demonstrating effects of alpha frequency on brief temporal judgments in the two-flash discrimination task (Coffin & Ganz, 1977; Samaha & Postle, 2015). This may suggest that the oscillatory phase cycle, and therefore its length, is important for sub-cycle organisation of temporal relations, for instance binding two stimuli that occur within one part of the cycle (Varela et al., 1981), but their ongoing rate may not continue to influence relative temporal judgments over longer durations (even sub-second). Accordingly, the results presented here do not mean that the framing hypothesis is an inaccurate account of phase effects at fine timescales, but they may suggest that framing, if true, does not influence the temporal judgment of longer durations.

An effect of pre-stimulus phase on temporal judgment but not sensitivity to the task (e.g. PSE or slope) may reflect a functional account of phase that stresses its importance in initial engagement or receptivity to the

onset of a stimulus duration, but not necessarily in the ongoing representation of it. This is compatible with existing evidence of pre-stimulus phase effects on the probability of liminal stimulus detection (Busch et al., 2009; Mathewson et al., 2009) and fine-grained temporal judgments (e.g. Baumgarten et al., 2015; Cravo et al., 2015) where all stimulus information was presented and contained within close temporal proximity to stimulus onset. One account of these findings might be that suboptimal phases at onset of a stimulus lead to a slower or less efficient neuronal reception. For timing tasks, this may relate to a latency delay in initiating a clock or in engaging related timing processes. Changes in the state of this initial neuronal reception may have repercussions for perceptual experiences of onset or fine-grained temporal relations without influencing ongoing conscious experience or sensitivity. For instance, a runner rocking on their feet at the starting line may be more likely to set-off quickly if the firing-gun coincides with a forward rock, but this initial rocking does not govern their actions during the rest of the race, even though it may exert a small influence on their final race time. If phase effects reflect fluctuation in the initial engagement or sampling of a stimulus, then the overall importance of such an effect to stimulus processing and task outcome should diminish as relevant stimulus information persists over longer durations. This would be compatible with the modest effect of phase reported on task outcome in this study (16%), and the general conception that interval timing is not a simple and singular process, but instead involves multiple stages and decision processes (Kononowicz et al., *in press*).

Another possibility is that pre-stimulus phase influences the memory component involved in the relative judgment of duration. A previous study has shown pre-stimulus phase can influence accuracy in a working memory task (Myers, Stokes, Walther, & Nobre, 2014). The authors suggested phase may have influenced initial encoding of a stimulus and in this way biased subsequent accuracy. This idea that phase may influence the memory rather than the perceptual aspect of the decision is compatible with the lack of relationship reported in this study between phase and the slope of participants' psychometric function for duration discrimination. However, perceptual, timing or memory accounts of the effect of pre-stimulus phase all suggest that the state of dynamic systems preceding stimulus onset can have long-lasting effects on the flow of processes that ultimately inform the experience of its duration. Though

the mechanism of influence remains to be determined, our results are in agreement with the idea that interval timing involves ballistic processes whose starting points are related to the outcome (Kononowicz & van Rijn, 2015).

Fluctuations in neuronal excitability represent periodic windows of opportunity in brain activity with functional repercussions for behavioural outcomes. This study presents novel findings that the phase of neuronal oscillations modulates temporal judgments persisting over several phase cycles. It is hoped that further exploration of conjoint phase and frequency effects will help resolve the role that both frequency and phase play in processing and perceiving events over time.

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